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TITLE I. VISUAL EVOKED RESPONSES TO SINUSOIDAL GRATINGS PRESENTED IN CENTRAL AND RIGHT VISUAL FIELDS

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I. VISUAL EVOKED RESPONSES TO SINUSOIDAL GRATINGS PRESENTED IN CENTRAL AND RIGHT VISUAL FIELDS

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INTRODUCTION

The present study applies neuromagnetic measurement techniques to probe the neurophysiological processing of spatial frequency. (SF) by normal human observers. By exploiting the temporal and spatial resolution of neuromagnetic measurements, we hope to discriminate and characterize underlying neural functions and explore their correlation with perceptual or behavioral performance measures. Spatial frequency analysis has proven a useful paradigm for the study of visual perception and has been applied in psychophysical studies as well as invasive anatomical and physiological studies of experimental animals (1). These approaches have produced evidence of specialized neural activity and network structure for the analysis of spatial frequency information. Because the encoding of spatial frequency is a function of neuronal receptive-field size and since receptive-field size varies as a function of retinal location, we have also examined effects of visual field on responses to stimuli of defined spatial frequency content.

Results obtained in single-unit studies of feline retinal gangtion cells suggests that the visual system contains two or more classes of neurons which differ in their receptive field (RF) and signal transmission characteristics (2,3). "Y" type neurons have larger RFs and respond best to lower spatial frequencies (~1 cycle per degree) while "X" cells have smaller RFs and respond best to frequencies > 1cpd. "Y" cells are typically larger and have faster conduction velocities than "X"-type cells. Within the retina, receptive-field size tends to increase from foveal to peripheral retinal areas, and there is a corresponding shift in the ratio of "X" to "Y" cells. The central retina has a higher proportion of "X" cells while the peripheral retina has more "Y" cells. In primates, analogous differences are observed between "magnocellular" and "parvocellular" cortical neurons.

Human psychophysical studies support the concept of spatial frequency selective channels within the human visual system (4). Observer's detection thresholds are lower for 5-10 cpd frequency gratings presented to the cantral retinal and for spatial frequencies around 1 cpd in the peripheral retina. Contrast sensitivity to high and low spatial frequency gratings is differentially affected by light adaptation, so that at lower light levels, peak contrast sensitivity shifts to lower spatial frequencies. The time-course of adaptation effects produced by presentation of a grating varies as a function of spatial frequency of the grating, again suggesting differences in the functional characteristics of the neural pathways mediating the responses.

Spatial frequency selective channels have been demonstrated in cat and primates by imaging the distribution of uptake of ¹⁴C 2-deoxyglucose under conditions of controlled visual stimulation. When spatial frequency was kept constant and other stimulus parameters varied, columnar structure, apparent in cross section as bands or blob patterns, could be visualized in striate tissue and in area V2 (5,6). This structure reflects neural organizational principles also associated with ocular dominance, orientation selective and other feature specific information channels (7).

Based on psychophysical and neurophysiological data, we expect an interaction between spatial frequency and field of stimulus presentation. Specific hypotheses include: 1) Responses to a 5 cpd grating presented in the central retina should be of greater magnitude than responses to a 1 cpd grating in the central visual field: 2) Responses to a 1 cpd grating presented in the peripheral retina should be of greater magnitude than responses to a 5 cpd grating presented in the same location; and 3) Responses to LO SF gratings and/or stimuli presented in peripheral visual fields should have shorter latencies than HI SF or contral stimuli.

METHODS

Two right-handed males and two right-handed females participated in the study. Sinusoidal gratings (1 and 5 cpd, LO and HI SF), each subtending 2 degrees (h) x 1.5 degrees(v) of visual angle were presented randomly to the central visual field (CVF) or to a location centered around 7 degrees in the right visual field (RVF). Rastered images rendered in 16 grey levels were generated by microcomputer and displayed on a rear-projection screen with a video projector. Subjects viewed the screen via a system of mirrors which allowed experimental access to the occipital region of the head. Stimulus duration was 100 msec and prestimulus data collection interval was 110 msec. Subjects were instructed to fixate on a small dot in the central visual field, and to count and classify each stimulus type in an effort to maintain a constant level of attention across thats.

Experiments were conducted in an aluminum and mumetal magnetically shielded chamber developed at Los Alamos in collaboration with Vacuumschmeltze, Hanau, West Germany. Neuromagnetic responses were monitored with a 7-channel SQUID-coupled gradiometer system (BTi, San Diego). Sensors were located on a 2 cm equilateral triangular grid (i.e., the center and vertices of a regular hexagon). Measurements were made at 6 contiguous array locations which nominally constituted an equilateral grid of 32 separate sensor locations.

At least two blocks of trials, consisting of an average of 25 responses to each of 4 stimulus conditions, were collected at each sensor location. Data channels were low-pass filtered at 50 Hz and subsequently digitized at a 1 kHz sampling rate. Visual evoked response data was typically processed with a digital FFT-based 30 Hz low-pass filter to remove residual 60 Hz signal arising from the vertical drive of the phase locked video signal. Statistical tests (MANOVAs and ANOVAs) were performed on measures of amplitude obtained at 13 time points, selected as best representing response features in the waveforms.

RESULTS

As expected from the retinotopic mapping of the primary visual cortex, we observed major differences in magnetic field distribution as a function of the visual field of stimulation. Figure 1 shows isofield contour maps at the peak of an initial magnetic response component peaking between 90 and 115 msec post-stimulus. For the LO CVF stimulus, the field polarity reverses across midline, consistent with a shallow source near the occipital pole. Secondary peaks are also apparent in the distribution; stimuli were not confined to a single quadrant of the visual field and would therefore be expected to activate multiple cortical representations. The fact that CVF stimuli produce a predominant dipole-like field distribution suggests that a significant degree of signal cancellation may be occurring. A central stimulus would be expected to activate an extended representation along opposing surfaces of the calcarine and longitudinal fissures, and might therefore produce an even more complex field pattern. In this subject, RVF timulation produced a single clear field extremum, although in this record there is a suggestion of an inversion near the periphery of the recording region, similar to that observed by Kaufman and Williamson (8). This distribution would be consistent with a source located several cm off midline, perhaps near the end of the calcarine fissue as suggested by the cruciform model (9,10). In two other subjects, a vertically aligned biphasic pattern in response to RVF stimulation was observed, while in the fourth subject the distribution of peripheral response components was not clear due to low amplitude and complex structure of the response.

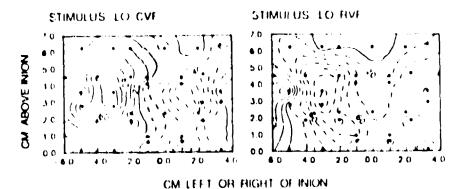


FIGURE 1
Isofield contour maps at the peak
of an early response continonent
Stimuli were 1 cpd solutioidal
gratings presented in the central
or right visual fields. Asterniks
mark locations of individual
sensors. LO CVF map is 90 mile,
and LO RVF is 115 misec
post stimulus.

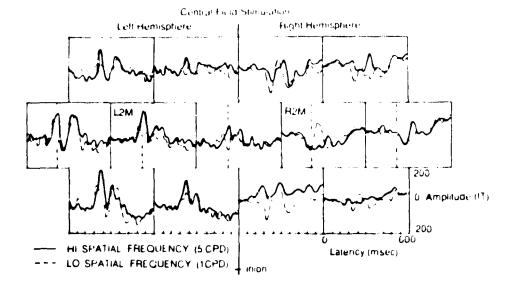


FIG. PE 2 Evoked response waveforms for LO and HI CVF stimulic objected at two adjacent sensor array locations (L2M and R2M in our nomenclature). Figure layout illustrates relative locations of sensors.

Upon initial inspection, field maps for 1 or 5 cpd stimuli at a particular location in the visual field appeared similar, with comparable features in the same general location. Upon closer inspection we noticed that a difference in spatial frequency sometimes produced a shift in apparent source location of early response components. This shift was most apparent for central field stimulation, and in most subjects appeared as a small shift in the location of response field extrema or an apparent crossover point. Figure 2 is a montage of response waveforms obtained in one subject at a series of adjacent sensor locations. Waveforms within any particular box were obtained simultaneously during randomly interleaved trials. Note that there is a clear separation of the location of the inversion of an early response component for high and low spatial frequency stimuli. In at least two other subjects, ratios of the amplitudes of response components between approximately 100 and 300 msec poststimulus varied significantly as a function of spatial frequency, suggesting that discrete secondary processing pathways may have been activated. However, high and low spatial frequency stimuli in RVF typically produced similar patterns which could be reasonably matched by scaling and offset adjustments.

In order to test our hypotheses concerning the interaction between spatial frequency and field of stimulation, response amplitude measures at selected time points were compared. In each subject we were able to identify a pair of sensor locations which included maximal and near maximalresponses for both high and low spatial frequencies for a particular field of stimulation. Measured amplitudes for these locations were averaged (although similar results were obtained when only the extrema locations were compared). Abstracted waveforms derived in this manner are illustrated in figure 3. Statistical analyses indicated that maximal responses to 5 cpd. gratings were of significantly greater amplitude in all subjects when presented to the central visual field, while the LO SF grating (1cpd) elicited a larger response with peripheral stimulation. The ratio between amplitudes of corresponding components of responses to HI and LO SF varied as a function of sensor location for CVF stimuli. For RVF stimulation, LO SF elicited larger responses for almost all components and sensor locations.

DISCUSSION

We observed major differences in apparent source location as a function of visual field of stimulation, as expected given the known retinotopic organization of the cortex and the spatial resolution of the neuromagnetic measurement technique. We were not able to localize the neural source for peripheral stimulation in all subjects due to physical constraints of our current experimental setup. Most field maps suggested activation of multiple neural sources; stimuli were designed for comparison with psychophysical and electrical evoked response paradigms, and were not optimized to produce focal neural activity. We were concerned about the possibility of eye movement or fixation errors contributing to observed differences in signals, however control experiments indicate that this is not a problem in this experimental series.

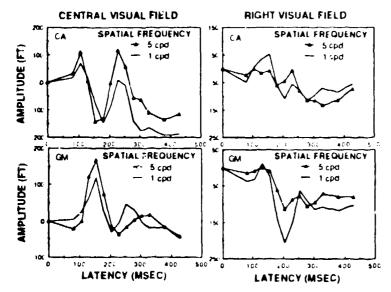


FIGURE 3
Abstracted waveforms
illustrating variation in
response amplitudes as a
function of spatial frequency and
visual field of stimulus
Waveforms are averages from
two sensor locations (at and near
an extremum for the initial
response component)

We observed a small but consistent shift in apparent source location as a function of spatial frequency. Even given the modular micro-organization of primary visual cortex (hypercolumns incorporating a number of specialized feature channels forming a retinotopic mosaic) we were surprised to detect differences. This observation suggests significant net asymmetry in the distribution of spatial frequency selective channels within an active cortical region. Such asymmetry might be enhanced by the geometry of the tightly curved cortical surface; small source shifts in the plane of the cortex could produce significant changes in orientation, producing a different mixture of radial and tangential components. Shifts in the location of longer latency peaks suggests that spatial frequency information can selectively activate secondary cortical sources. The observation that processing differences as a function of spatial frequency were most apparent in CVF may be significant. In the autoradiographic studies in cat (10), high spatial frequency channels were only observed in the certical projections of the central 5 degrees of visual field.

The observed interaction between the effects of spatial frequency and field of stimulation on response amplitudes supports our hypothesis based on the distribution of cell types and receptive-field sizes in retinal neurons. Apparent neural source locations also appear consistent with the known physiology and anatomy of the visual system. The observed shift in apparent source location as a function of spatial frequency was unexpected but may reflect the orderly columnar structure of spatial frequency channels demonstrated in visual cortical areas of experimental animals. However, in this experiment we did not consistently observe the predicted differences in esponse latency associated with spatial frequency or field of stimulation. This issue is addressed further in a subsequent study (Aine et al., this volume).

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